OBSERVATIONS ON *LITHOPHYLLUM LICHENOIDES* PHILIPPI (RHODOPHYTA, CORALLINACEAE) AND ITS REPRODUCTIVE STRUCTURES.

Yvonne M. CHAMBERLAIN

Institute of Marine Sciences, University of Portsmouth, Ferry Road, Portsmouth, PO4 9LY, U.K.

ABSTRACT -- *Lithophyllum lichenoides* Philippi (Rhodophyta, Corallinaceae) is a common, intertidal to shallow subtidal, nongeniculate, coralline red alga on the western Mediterranean and the Atlantic coasts of France and Spain. Its external appearance and vegetative anatomy are well known but little information is available with respect to its reproductive anatomy. Based on recently collected plants from northern Spain and Mediterranean France a description is given of vegetative, spermatangial, carpogonial/ carposporophytic and tetrasporangial structures. Pore-blocking cells are present in tetrasporangial conceptacles.

RÉSUMÉ — *Lithophyllum lichenoides* (Rhodophyta, Corallinaceae) est une algue rouge, coralline, non-articulée, commune, qu'on trouve dans la zone de ressac, un peu au dessus du niveau, le long des côtes de la Méditerranée occidentale et des côtes atlantiques de France et d'Espagne. Son apparence externe et son anatomie végétative sont bien connues mais on a peu de renseignements quant aux caractères de sa reproduction. On donne ici une description (basée sur des thalles récoltés récemment au nord de l'Espagne et en France méditerranéenne) de ses structures végétatives, de celles des spermatocystes, des carpogones/carposporocystes et des tétrasporocystes. Des cellules bloquant les pores sont présentes dans les conceptacles à tétraspores.

KEY WORDS: Rhodophyta, Corallinaceae, *Lithophyllum lichenoides*, reproductive structures

INTRODUCTION

Lithophyllum lichenoides Philippi (Rhodophyta, Corallinaceae) is a common, intertidal to shallow subtidal, nongeniculate coralline alga. It occurs commonly in the western Mediterranean and in Atlantic France and Spain. It has also been recorded (Ardré *et al.*, 1973) from the Azores. The species figures prominently in many floristic and ecological studies (e.g. Feldmann 1942; Cabioch *et al.*, 1992) and previously published ecological observations are summarised. Despite its abundance, the only descriptions and illustrations of its reproductive structures are those by Rosanoff (1866, pl. VII, figs 5, 7, 8 as *L. crassum*) which show little detail; by Huvé (1957, figs 1, 2 — as *L. tortuosum*) which show some features of tetrasporangial conceptacles; and illustrations by Woelkerling (1983, figs 24-32) of the lectotype in which little reproductive detail is visible because of the condition of the long-dried material. No description of gametangial plants has been published. The present study is based on plants collected at Cabo Higuer, northern Spain. Thallus anatomy and reproductive structures were examined and compared with those of other species of *Lithophyllum*. Further plants from Mediterranean France, including Corsica, were also examined. Masaki (1968) recorded *L. lichenoides* (as *L. tortuosum*) from middle Japan and presented detailed descriptions of gametangial and tetrasporangial reproductive structures. The vegetative and reproductive features of European plants are compared with those of Japanese plants as described by Masaki (1968).

MATERIAL AND METHODS

Air dried plants were decalcified for sectioning with Perenyi's fluid (4 parts 10 % nitric acid: 3 parts 90 % ethanol: 3 parts 0.5 % chromic acid), the thallus was hardened in 80 % ethanol and sectioned at 10-20 µm thickness on a Mectron freezing microtome. Sections were mounted on a microscope slide in 50 % Karo® corn syrup coloured with aniline blue. For scanning electron microscopy specimens were rinsed in demineralised water and air dried. Whole thalli or fractures were mounted on double sided sticky tape, coated with gold/palladium and examined in a Jeol T20 scanning electron microscope at 20KV. In cell measurements, length denotes the distance between primary pit connections and diameter the width of the cell lumen at right angles to this. Conceptacle measurements follow the method adopted by Adey & Adey (1973). Thallus terminology follows Chamberlain (1990) for the monomerous thallus in which the multistratose lower filaments are termed the medulla and the filaments derived peripherally from these the cortex. In the dimerous thallus the lowermost, unistratose layer is termed basal filaments and the upper filaments at right angles to these are the erect filaments. Drawings are made by the author on the basis of individual slide preparations and are not composite representations. VS = vertical section; YMC 89/303 etc. are the author's collection numbers.

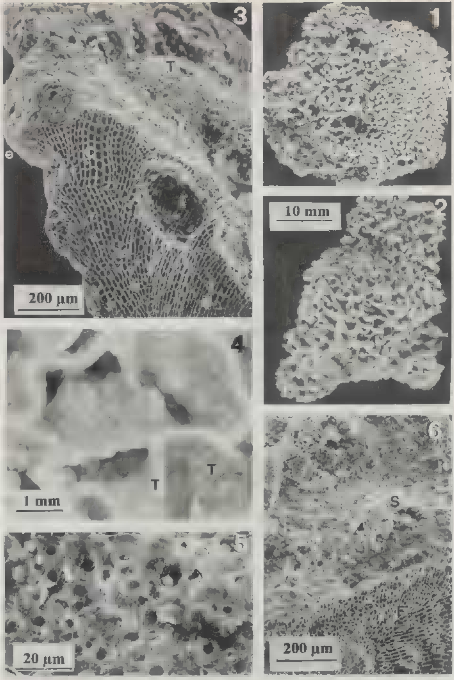
Collections examined: Spain: Cabo Higuer, Bay of Biscay, Vascongadas (YMC, 24.x.1988, YMC 88/99); France: Le Dromont, Var., part of a 'trottoir' (*E. Coppejans*, vi.1969, YMC 83/309); St Cyr sur Mer, Bouches du Rhone, subtidal and exposed to strong wave action (*M. Prior*, 30.iii.1996, YMC 96/27); Calvi, Corsica, mid to low littoral, forming large concretions (*E. Coppejans*, 23.viii.1983, YMC 84/36).

OBSERVATIONS

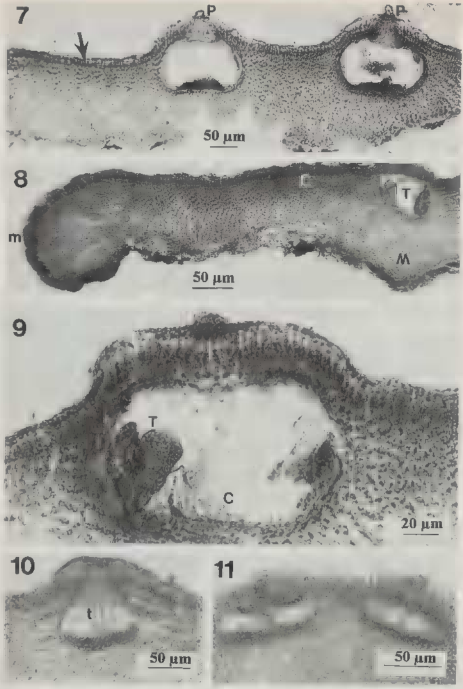
Lithophyllum lichenoides Philippi, 1837: 389.

Heterotypic synonyms: *Lithophyllum cristatum* Meneghini (1840: 512) *fide* Hamel & Lemoine, 1953: 67; *L. crassum* Rosanoff (1866: 93) non Lloyd (in herb. CHE no. 318); *L. tortuosum* auct. *sensu* Lemoine, non *Tenarea tortuosa* Esper.

At Cabo Higuer, *Lithophyllum lichenoides* grows commonly on rocks in the intertidal zone. It forms cushion-like clumps (Fig. 2) up to about 20 mm high that are composed of erect lamellae (Fig. 4) united into a complex, densely interweaving and anastomosing honeycomb-like mass. The lamellae are up to 800 µm thick. They are more or less smooth on the dorsal surface and ridged on the ventral surface. When moist the plants are not easily damaged, but they become brittle and fragile when dried. Plants are



Figs 1-6. Habit of *Lithophyllum lichenoides*. Fig. 1. Thallus with finger-like protuberances (YMC 83/309). Scale as in Fig. 2. Figs 2-6. Specimen YMC 88/99, from Cabo Higuer. Fig. 2. Thallus with erect lamellae. Fig. 3. Vertical fracture showing upper edge (e) of the thallus, cortical filaments (C) in vertical fracture and tetrasporangial conceptacles (T) in surface view and vertical fracture (t). Fig. 4. Erect lamellae with tetrasporangial conceptacles on both surfaces. Fig. 5. Thallus surface. Fig. 6. Spermatangial thallus showing conceptacles (S) with a central spout (arrow) in surface view and the thallus in vertical fracture (F).

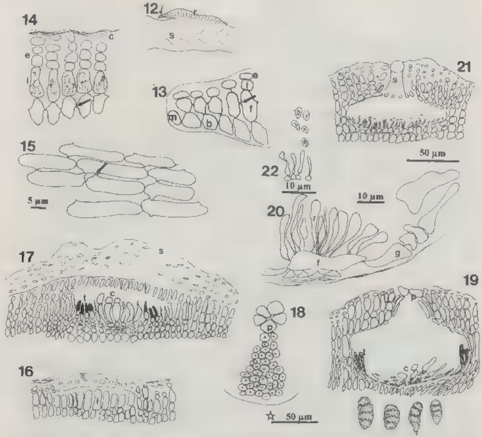


Figs 7-11. Vertical sections showing thallus and reproductive structures of *Lithophyllum lichenoides* (YMC 88/99). Fig. 7. Thallus with two immature carposporangial conceptacles, note pore plugs (P) and conspicuous subepithallial initials (arrow). Fig. 8. Thallus with tetrasporangial conceptacle (T) containing tetrasporangia, note thallus margin (m), cortical filaments (C) and medullary filaments (M). Fig. 9. Tetrasporangial conceptacle, note tetrasporangia (T) and columella (C). Fig. 10. Carpogonial conceptacle with trichogynes (t). Fig. 11. Two spermatangial conceptacles with spout-like pores.

dull mauve and the thallus surface is matt. Under the SEM the surface (Fig. 5) mainly shows a *Phymatolithon*-type structure (Chamberlain 1990) with calcareous ridges surrounding epithallial concavities, but due to cell shedding the appearance is often irregular and disordered. Both sides of most lamellae are covered with uniporate, low-domed conceptacles (Figs 4, 6), carposporangial and tetrasporangial conceptacles measure up to 250 μm in outside diameter, spermatangial ones measure up to 160 μm in outside diameter.

Vegetative anatomy: The thallus is presumably initially dimerous but no very young thalli can be seen. However, thallus regeneration (Figs 12) over dead thallus areas occurs frequently. This often results in the production of regenerating margins (Figs 12, 13) which are assumed to show the same type of margin as would be seen in the initial thallus. A dimerous *Lithophyllum* type of structure (Fig. 13) develops in which a single terminal cell is present and the thallus thickens immediately behind this cell (Fig. 13). This structure is similar to that seen in *L. incrustans* Philippi, the type species of *Lithophyllum* (see Woelkerling, 1983, figs 18-20). Basal filament cells and erect filament cells (Fig. 13) are squarish to elongate and subepithallial cells (Fig. 13) are elongate. Epithallial cells mainly occur singly and are small and inconspicuous (Fig. 13). Secondary, monomerous thalli (the 'faux hypothalle' of Cabioch, 1972) comprise the main bulk of the plants. The thallus meristem (Figs 3, 8) occurs at the apices of lamellae and is composed of elongate, densely staining cells that terminate in small, irregular epithallial cells. The meristem gives rise ventrally to downward-curving, medullary filaments (Figs 8, 15) of elongate cells that measure 11-25 μm long x 6-9 μm in diameter. Medullary filaments do not terminate in epithallial cells. Cortical filaments of squarish to elongate cells develop dorsally (Figs 3, 8), the cells measure 4-9 μm long x 4-18 μm in diameter. Subepithallial initials (Fig. 14) are conspicuous, they are relatively long and thin and measure 12-20 μm long x 3-7 μm in diameter. The upper half of each initial is particularly densely-staining and in sections they collectively appear as a dark band (Fig. 7) just below the dorsal surface. Epithallial cells appear to be very fragile. When intact (Fig. 14) they occur in up to four layers of small, squarish cells that measure 4-6 μm long x 3-6 μm in diameter, but they are frequently absent or damaged and difficult to see. Epithallial cells immediately above subepithallial initials are apparently living (Fig. 14), but those nearer the surface appear to be senescent. Secondary pit connections occur between thallus cells of contiguous filaments (Figs 13-15), cell fusions were not seen. No trichocytes were seen.

Reproduction: Gametangial thalli are dioecious. Spermatangial conceptacle chambers (Figs 11, 21) are low elliptical and measure 83-130 μm in diameter x 36-52 μm high. The roof is 21-36 μm thick and is composed of filaments up to four cells long; the conceptacle pore is tube-like and sometimes extended into a spout (Figs 6, 11, 21). Simple spermatangial systems occur only on the floor of the chamber (Fig. 22). Carpogonial conceptacle chambers (Fig. 10) are flask-shaped, they measure 95-100 μm high x c. 90 μm in diameter, the roof pore is about 20 μm long. Carpogonia develop on the chamber floor and long, conspicuous trichogynes extend to the pore of the conceptacle (Fig. 10). Carpogonial branches are borne on supporting cells and mainly comprise a hypogynous cell and a carpogonium extending into a trichogyne; a sterile cell or second carpogonium sometimes occurs. After presumed fertilisation, a fusion cell develops on the conceptacle floor and gonimoblast filaments develop peripherally (Fig. 20). The conceptacle roof becomes domed and is composed of filaments of elongate cells up to three cells long. Cells surrounding the pore (Fig. 7) are slightly papillate and a (possibly mucilaginous) pore plug develops. The carposporangial conceptacle chamber (Fig. 7) measures c. 97 μm high x 155 μm in diameter, with the roof 21-36 μm thick.



Figs 12-22. Vertical sections showing thallus and reproductive structures of *Lithophyllum lichenoides* (YMC 88/99). Scale with asterisk applies to Figs 16-19. Fig. 12. Diagrammatic drawing of senescent lamella (s) with cortical regeneration dorsally (r) and regenerating margin overgrowing the old thallus (arrow) 7 mm = 100 µm. Figs 13-15. Representative thallus cells, arrows indicate secondary pit connections. Fig. 13. Regenerating thallus margin (see Fig. 12) showing dimerous structure with marginal initial (m), basal filament cells (b), erect filament cells (f), subepithallial initials (i) and epithallial cells (e). Scale as Fig. 15. Fig. 14. Upper thallus of a monomerous lamella showing subepithallial initials (i), epithallial cells (e) of which only the lowermost are living, and shedding cuticle and uppermost epithallial cells (c). Scale as Fig. 15. Fig. 15. Medullary cells in centre of a monomerous lamella. Figs 16-19. Tetrasporangial conceptacles: starred scale applies to all these figures. Fig. 16. Conceptacle initiation commencing in swollen subepithallial initials (i) and old epithallial layers being shed (s). Fig. 17. Later stage of conceptacle development with roof being formed from subepithallial initials (i), old epithallial layers being shed (s), tetrasporangial initials (t) developing peripherally, and a central columella (c). Fig. 18. View of mature conceptacle roof from above with central pore cells (p) and small roof cells. Fig. 19. Mature conceptacle with young tetrasporangia (t), columella (c), and pore cells (p); four tetrasporangia have been extruded. Fig. 20. Part of a nearly mature carposporangial conceptacle showing the fusion cell (f) bearing carpogonial remnants (r) on the surface and a young gonimoblast filament (g) peripherally. Fig. 21. Spermatangial conceptacle with a spout-like pore (s). Fig. 22. Detail of simple spermatangial systems and released spermatangia.

Bisporangial plants are unknown. Stages in tetrasporangial conceptacle development show that conceptacles are initiated (Fig. 16) when a group of subepithallial initials become enlarged. The epithallial layer above these cells is eventually shed (Fig. 17) and the subepithallial initials develop into the conceptacle roof. At this stage (Fig.17) a central columella has developed and tetrasporangial initials occur in a peripheral ring. Mature tetrasporangial conceptacle chambers (Figs 9, 19) are elliptical, in VS they measure 65-91 µm high x 138-156 µm in diameter, they are overlain by a roof that is 21-36 µm thick. The chamber floor is situated about 5-8 cells below the thallus surface (Fig. 19). The roof (Figs 9, 19) is two to three cells thick and is composed of an epithallial cell and one or two elongate or squarish cells. The mature pore (Fig.19) is surrounded on each side by one or two vertically oriented thin cells with two large hyaline cells (Fig. 19) apparently blocking the pore at the thallus surface. In surface view (Fig. 18) there are 5-7 of these pore-blocking cells round each pore. Tetrasporangia develop peripherally on the conceptacle floor (Fig. 9) and an insubstantial columella is present in the centre of the floor (Figs 9, 19). Most conceptacles present appeared to lack a columella and it seems that only strictly radial sections show this structure. Mature tetrasporangia measure 22-32 µm long x 7-9 µm in diameter.

Old spermatangial conceptacles may become buried in the thallus but old carposporangial and tetrasporangial conceptacles are shed and do not become buried.

COMPARISON OF SPECIMENS

Specimens examined show consistent vegetative and reproductive anatomical characters. Three somewhat distinct morphological forms were noted. The specimens from Cabo Higuer (YMC 88/99) occurred as scattered plants on intertidal rocks and showed an erect, lamellate structure (Figs 2, 4). Another form (YMC 83/309) comprised clumps of closely interlocking, finger-like protuberances (Fig. 1). Specimens from a particularly wave-exposed locality near Marseille (YMC 96/27) showed a mainly crustose plant with small, warty protuberances up to about 2 mm high. Either of the first two forms apparently builds up the huge concretions or 'trottoirs' (e.g. Cabioch *et al.*, 1992, figs 232, 233) that are a feature of Mediterranean shores.

The plants collected at Cabo Higuer had lamellae that were covered with uniporate conceptacles on both surfaces (Fig. 4). In other populations, however, while the thallus surface was covered with minute bumps, conceptacles were very hard to find and the bumps were purely vegetative in origin.

NOMENCLATURE

The nomenclature of plants now attributed to *Lithophyllum lichenoides* had become complicated until it was clarified by Woelkerling (1983) when he established *L. lichenoides* Philippi (1837) as the earliest name for this species. After Philippi's original description, Meneghini (1840) described *L. cristatum* from Genoa, Italy which is now considered to be conspecific with *L. lichenoides* (Hamel & Lemoine, 1953: 67). Rosanoff (1866) took up Lloyd's species *Melobesia crassum* (in herb. CHE, no. 318). I examined no. 318, however, and found it to be *Mesophyllum lichenoides* (Ellis) Lemoine. Nevertheless, the name has subsequently been used for coarse forms of *Lithophyllum lichenoides* and

Source : MNHN, Paris

Rosanoff's own description and illustrations (1866, pl. VII, figs 5, 7, 8) of *L. crassum*, apparently based on other specimens, agrees well with *L. lichenoides*.

For many years the identity of the 'trottoir' plant *Lithophyllum lichenoides* was confused with the morphologically similar species from Greece first described by Esper (1796) as *Millepora tortuosa* and renamed by Bory (1832) as *Tenarea undulosa*. This species is now known as *T. tortuosa* (Esper) Lemoine for reasons discussed in Woelkerling *et al.* (1985). Esper's type was mislaid for many years and it was not until Woelkerling *et al.* (1985) rediscovered it in Senckenberg Museum that it was possible to prove that Esper's and Bory's plants were conspecific and that they differed taxonomically from the 'trottoir' plant. The intermediate nomenclatural complexities are documented in Foslie (1898), Lemoine (1910, 1911), Huvé (1957), Adey (1965), Woelkerling (1983) and Woelkerling *et al.* (1985).

A further complication arose when the identity of *Lithophyllum lichenoides* became confused with the species now known as *Mesophyllum lichenoides* (Ellis) Lemoine, a member of the subfamily Melobesioideae, apparently simply because of the similarity of names. This matter is documented in Woelkerling (1983). The nomenclature of *Lithophyllum lichenoides* is now under further review in conjunction with a study of nongeniculate coralline type collections at the Muséum National d'Histoire Naturelle (Dr Woelkerling, personal communication).

ECOLOGICAL OBSERVATIONS

Populations of *Lithophyllum lichenoides* form one of the most familiar shore features in many areas of the Mediterranean (e.g. Morhange *et al.*, 1992) where they create massive concretions ('trottoirs') at the low intertidal/subtidal interface (e.g. Feldmann, 1942; Hamel & Lemoine, 1953 — both as *Tenarea tortuosa*; Huvé, 1963; Augier & Boudouresque, 1967; Gayral, 1958; Bressan, 1974; Cormaci & Furnari, 1979; Cabioch *et al.*, 1992 — all as *Lithophyllum tortuosum*). Cabioch *et al.* (1992) show a massive population (figs 232-233) and illustrate individual plants (fig. 231) that closely resemble those illustrated in this paper (Figs 1, 2). This species is also common on the Atlantic coasts of France (e.g. Lancelot, 1964, as *L. tortuosum*) and Spain where, for example, Hoek & Donze (1966 — as *L. tortuosum*) describe it as dominating a mid tide subzone of the Côte Basque. Ardré *et al.* (1973) record *L. lichenoides* on the Azores where it occurs on very wave-exposed shores.

Laborel *et al.* (1994) used the present and past positions of the 'trottoir' in the western Mediterranean to indicate recent sea-level variations in that area. They concluded that sea level had risen about 1.6 m during the last 4500 years. Morhange *et al.* (1993) showed that the rate of sea level rise on the coast of Provence, France, had been constantly decreasing over the past 5000 years and had ceased in the region about 500 years ago.

P. Huvé (1954, 1956 — as *Tenarea tortuosa*) studied the regeneration of cleared colonies in the Golfe de Marseille. Within two years there was nearly 100 % cover of *L. lichenoides* and plants were about 1 cm high. Boudouresque *et al.* (1972 — as *L. tortuosum*) studied the growth rate of tagged plants at Port Cros and found that young plants grew as much as 1.5 mm in height per month. Growth rate slowed with age but volume gain remained consistent so that, for example, a 60 mm high plant could be identified as being 2-3 years old.

DISCUSSION

Cabo Higuer plants of *Lithophyllum lichenoides* agree well with the habit and vegetative anatomy of the lectotype as re-described by Woelkerling (1983). Woelkerling was unable to make detailed observations of reproductive anatomy because of the condition of the material. The present results, however conform to his recorded dimensions and Woelkerling (1983, fig. 32) also noted the presence of some sort of pore-blocking mechanism but was unable to determine whether the conceptacle he examined was carposporangial or tetrasporangial. This possibly corresponds with the pore plug seen in carposporangial conceptacles in the present study (Fig. 7). Thallus and tetrasporangial conceptacle structure also agree well with the illustration by Rosanoff (1866, pl. VII, fig. 7) although he did not observe pore-blocking cells.

Japanese plants described by Masaki (1968, as *L. tortuosum*) differ from the present plants in having ventral struts (termed rhizoids by Masaki) below the thallus. It is not known whether pore-blocking cells are present in the tetrasporangial conceptacles of Japanese plants and until this information is available, it is not possible to assess whether European and Japanese plants are conspecific.

In most species of *Lithophyllum* tetrasporangial conceptacle pore canals are lined by small papillae that are aligned more or less parallel to the thallus surface. However, a number of species were noted by Woelkerling & Campbell (1992) to have pore-blocking cells of various shapes. Most of the species in which these occurred would be attributed by the present author to the genus *Titanoderma*. However, various *Lithophyllum sensu stricto* species have since been shown to have either pore-blocking cells or elongate cells that are vertically oriented immediately surrounding the pore canal. Pore-blocking cells occur in *L. crouanii* Foslie (Chamberlain & Irvine 1994, fig. 21F) and *L. johansenii* Woelkerling & Campbell (1992, figs 39C, 39D). Both of these species differ from *L. lichenoides* in having strictly dimerous thalli, in having layers of old, buried tetrasporangial conceptacles and in lacking a central columella in tetrasporangial conceptacles.

Vertically oriented surrounding cells are seen in the holotype (!), from Japan, of *L. neoatalayense* Masaki (1968) as well as in South African material of this species (Chamberlain, 1996). They also occur in *L. retusum* Foslie (Chamberlain, personal observation). The structure of these filaments is different from pore-blocking cells but resembles the thin filaments (Fig. 16) seen below the pore-blocking cells in mature conceptacles of *L. lichenoides*.

ACKNOWLEDGEMENTS — I am most grateful to M. Ancellin at Cherbourg (CHE) and Dr Sigmund Sivertsen at Trondheim (TRH) for the loan of herbarium material. Dr Eric Coppejans and Mr Matthew Prior very kindly gave me specimens they had collected. I am grateful to Colin Derrick and Graham Bremer for assistance with photography and SEM respectively. I appreciate permission from the School of Biological Sciences, University of Portsmouth, to work in the Institute of Marine Sciences. I am most grateful to two referees who made helpful suggestions for the improvement of this paper. I gratefully acknowledge assistance from the Botanical Research Fund.

It is with great pleasure that I dedicate this paper to Prof Françoise Ardré on her retirement and it is an honour to have been requested to contribute to this volume by Dr Bruno de Reviers. Prof Ardré has made a distinguished contribution to algal studies in her publications and has curated the algal herbarium at the Laboratoire de Cryptogamie for

many years. She has been most helpful to myself and many taxonomists in finding and mailing herbarium material very efficiently and promptly - a task greatly appreciated by the recipients.

REFERENCES

ADEY W.H., 1965 — The Lithophylleae. *In*: Johnson J.H. & Adey W.H. Studies of *Lithophyllum* and related genera. *Colorado School of Mines Quarterly* 60 (2): 71-102.

ADEY W.H. & ADEY P.J., 1973 — Studies on the biosystematics and ecology of the epilithic crustose Corallinaceae of the British Isles. *British Phycological Journal* 8: 343-407.

ARDRÉ F., BOUDOURESQUE C.-F. & CABIOCH J., 1973 — Note préliminaire sur la mission "Biaçores" du N.O. Jean Charcot (Algologie). *Bulletin de la Société phycologique de France* 18: 30-32.

AUGIER H. & BOUDOURESQUE C.-F., 1967 — Végétation marine de l'Ile de Port-Cros. I. La baie de La Palu. *Bulletin du Muséum d'Histoire naturelle de Marseille* 27: 93-124.

BORY DE SAINT-VINCENT J.-B., 1832 — Notice sur les polypiers de la Grèce. Expédition scientifique du Morée. *Sciences physiques* 3: 204-209.

BOUDOURESQUE C.-F., AUGIER H. & GUÉNON Y.-C., 1972 — Végétation marine de l'Ile de Port Cros. VIII. Premiers résultats de l'étude de la croissance *in situ* de *Lithophyllum tortuosum* (Rhodophycées, Corallinacées). *Bulletin du Muséum d'Histoire naturelle de Marseille* 32: 197-215.

BRESSAN G., 1974 — Rodoficee calcaree dei Mari Italiani. *Bolletino della Società Adriatica di Scienze naturali* LIX: 1-132.

CABIOCH J., 1972 — Étude sur les Corallinacéees. II. La morphogenèse; conséquences systématiques et phylogénétiques. *Cahiers de Biologie Marine* 13: 137-288.

CABIOCH J., FLOC'H J.-Y., LE TOQUIN A., BOUDOURESQUE C.-F., MEINESZ A. & VERLAQUE M., 1992 — *Guide des algues des mers d'Europe*. Paris, Delachaux & Niestlé, pp. 1-231.

CHAMBERLAIN Y.M., 1990 — The genus *Leptophytum* (Rhodophyta, Corallinaceae) in the British Isles with descriptions of *Leptophytum bornetii*, *L. elatum* sp. nov. and *L. laeve*. *British Phycological Journal* 25: 179-199.

CHAMBERLAIN Y.M., 1996 — The lithophylloid crustose coralline red algae of the genera *Lithophyllum* and *Titanoderma* from South Africa. *Phycologia* 35: 204-221.

CHAMBERLAIN Y.M. & IRVINE L.M., 1994 — Lithophylloideae. *In*: Irvine L.M. & Chamberlain Y.M., *Seaweeds of the British Isles*, Vol.1, Part 2B: 58-112, HMSO, London, British Museum (Natural History).

CORMACI M. & FURNARI G., 1979 — Flora algale della peninsola della Maddalena (Siracusa). *Thalassia Salentina* 9: 3-18.

ESPER E.J.C., 1796 — *Fortsetzungen der Pflanzenthiere in Abbildungen*. Volume 1, Parts 5-6, pp. 117-168. Raspe, Nürnburg.

FELDMANN J., 1942 — Les algues marines de la Côte des Albères IV — Rhodophycées. *Revue algologique* 11: 247-330.

FOSLIE M., 1898 — List of species of the *Lithothamnia*. *Kongelige norske Videnskabers Selskabs Skrifter* 1898 (3): 1-11.

GAYRAL P., 1958 — *La nature au Maroc. II. Algues de la côte Atlantique Marocaine*. Société des Sciences naturelle et physique du Maroc, Rabat. 523 p.

HAMEL G. & LEMOINE M., 1953 — Corallinacées de France et d'Afrique du Nord. *Archives du Museum National d'Histoire Naturelle, Paris*, Séries 7, 1: 15-136.

HOEK C. van den & DONZE M., 1966 — The algal vegetation of the rocky Côte Basque (SW France). *Bulletin du Centre d'Études et de Recherches Scientifiques Biarritz* 6: 289-319.

HUVÉ H., 1957 — Sur l'indiviualité générique du *Tenarea undulosa* Bory 1832 et *Tenarea tortuosa* (Esper) Lemoine. *Bulletin de la Société botanique de France* 104: 132-140.

HUVÉ H., 1963 — Données écologiques et biogéographiques relatives a quelques mélobésiées méditerranéennes caractéristiques des niveaux superficiels de la roche littorale. *Rapport et Procès-Verbaux des Réunions. Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée* 17: 147-160.

HUVÉ P., 1954 — Étude expérimentale de la réinstallation d'un "trottoir à *Tenarea*", en Méditerranée occidentale. *Comptes rendus Hebdomadaires des Séances de l'Académie des Sciences*, Paris. 239: 323-325.

HUVÉ P., 1956 -- Étude expérimentale de la réinstillation d'un "trottoir à *Tenarea*", en Méditerranée occidentale. *Comptes rendus Hebdomadaires des Séances de l'Académie des Sciences*, Paris, 243: 2157-2158.

LABOREL J., MORHANGE C., LAFONT R., LE CAMPION J., LABOREL-DEGUEN F. & SARTORETTO S., 1994 — Biological evidence of sea-level rise during the last 4500 years on the rocky coasts of continental south-western France and Corsica. *Marine Geology* 120: 203-223.

LANCELOT A., 1964 — Les algues Mélobésiées de Biarritz. *Proceedings of the International Seaweed Symposium*, Biarritz. 4: 226-233.

LEMOINE Mme P., 1910 — Essai de la classification des Mélobésiées basée sur la structure anatomique. *Bulletin de la Société botanique Française* 57: 323-331 and 367-372.

LEMOINE Mme P., 1911 — Structure anatomique des Mélobésiées. Application à la classification. *Annales de l'Institut Océanographique*. Monaco 2 (1): 1-213.

MASAKI T.,1968 -- Studies on the Melobesioideae of Japan. *Memoirs of the Faculty of Fisheries. Hokkaido University* 16: 1-80.

MENEGHINI G., 1840 -- *Lettera del Prof. Giuseppi Meneghini al Dott. Jacob Corinaldi a Pisa.* Tipografia Prosperi. Pisa, 3 p.

MORHANGE C., LABOREL J., LABOREL-DEGUEN F., LOUNNAS V. & VERRECCHIA E., 1993 — Indicateur biologique et variations relatives du niveau de la mer sur les côtes rocheuses de Provence depuis 4500 ans. *Géologie Méditerranéenne* 20 (2): 89-100.

MORHANGE C., LABOREL-DEGUEN F., SARTORETTO S. & LABOREL J., 1992 — Recherches sur les bioconstructions à *Lithophyllum lichenoides* en Mediterranée occidentale. *Méditerranée* 3: 67-71.

PHILIPPI R., 1837 — Beweis dass die Nulliporen sind. Archiv für Naturgeschichte 3: 387-393.

ROSANOFF S., 1866 — Recherche anatomique sur les Mélobésiées. *Memoires de la Société impériale des Sciences naturelles et mathématiques de Cherbourg* 12: 5-112.

WOELKERLING Wm J., 1983 — A taxonomic reassessment of *Lithophyllum* (Corallinaceae, Rhodophyta) based on studies of R.A. Philippi's original collections. *British Phycological Journal* 18: 299-328.

WOELKERLING Wm J. & CAMPBELL S.J., 1992 — An account of southern Australian species of *Lithophyllum* (Corallinaceae, Rhodophyta). *Bulletin of the British Museum (Natural History)*, Botany Series, 22: 1-107.

WOELKERLING Wm J., CHAMBERLAIN Y.M. & SILVA P.C., 1985 — A taxonomic and nomenclatural reassessment of *Tenarea, Titanoderma* and *Dermatolithon* (Corallinaceae, Rhodophyta) based on studies of type and other critical specimens. *Phycologia* 24: 317-337.